Phenology and Distribution of Some *Pterostichus* (Coleoptera: Carabidae) of Eastern Canada

C. A. Barlow

Department of Biology, Carleton University, Ottawa 1, Canada

Received for Publication August 29, 1970

Abstract: The seasonal occurrence and ecological distribution of five *Pterostichus* species were analyzed by pitfall trapping.

Two species, *melanarius* and *coracinus*, exhibited one activity-abundance cycle per year which extended from May or June to September or October. Reproduction occurred throughout most of this cycle. These species apparently overwinter both in the larval stage and as teneral adults. The remaining species, *pensylvanicus, lucublandus*, and *mutus,* each showed two cycles per year. The first extended from April to July during which reproduction occurred. A period of decreased abundance and activity in midsummer was followed by a second cycle of varying length and intensity between September and November. This was a non-productive cycle composed of progeny of the spring reproductive period. These three species apparently overwinter almost entirely as teneral adults.

P. pensylvanicus was taken mostly in wooded areas, while *lucublandus* occurred almost entirely in non-forested areas. The remaining species were found both in forest and open areas: *coracinus* principally in forest or forest edge, *mutus* also mainly in forest but also in some open areas, and *melanarius* mostly in grassland with some woods. No temporal or sexual difference in distribution was noted.

INTRODUCTION

The initial difficulty encountered in studying many insect populations is the paucity of information of the ecology and life-history of the species.

The genus *Pterostichus* Bon., often referred to as *Feronia* Lat. in Europe, represents one of the largest groups of the family Carabidae with worldwide distribution. Lindroth (1966) described 81 species for Canada alone. The present work reports part of the results of four years study on the phenology and ecological distribution of five of the most common species of eastern Canada: *P. melanarius* Ill., *P. coracinus* Newm., *P. pensylvanicus* Lec., *P. lucublandus* Say, and *P. mutus* Say. All are apparently native to North America except *melanarius* which has been introduced from Europe (Lindroth, 1966). The geographic distribution of *pensylvanicus* and *lucublandus* is almost transamerican; *melanarius* now extends over much of Canada. However, *coracinus* and *mutus* seem to be limited to the eastern half of the country.

Acknowledgments: The cooperation of Mr. R. E. Edey, Superintendent of Parks, National Capital Commission, Ottawa, is much appreciated. Technical assistance was received from Mr. D. J. van der Weyden.

EXPERIMENTAL AREA

The study was done in parts of Gatineau Park, a 35,600 hectare preserve near Ottawa. The area lies between the Gatineau River on the east and the Ottawa River on the west where the land, for much of its length, falls through an escarpment to the river valley. To the south, the elevation decreases gradually toward the Ottawa River.

Geologically, the area is composed of Precambrian metamorphic rock overlaid in places by rocks of Pleistocene and more recent origin. Because of its geologic nature, the area is generally rocky and the soil relatively shallow.

The climate of the study area is different from that of the surrounding valley due to the prevailing west wind in combination with the 150–300 m. elevation of its westward exposure. Average temperature in the area is several degrees lower, both summer and winter, than in the Ottawa valley which averages about 19.3°C. between June and August and –9.8°C. between December and February. Total yearly precipitation is several cm. higher than the average 86 to 87 cm. which falls in the neighboring valley. These conditions lead to considerable accumulation of snow in the study area. Average snow depths recorded in February, 1967 and 1968, were between 47 cm. and 70 cm.

Until the last century, Gatineau Park was almost entirely covered by mixed coniferous and deciduous forest including extensive stands of white pine. These have been virtually destroyed by logging and the area is now covered by deciduous trees. Open areas have been produced by farming, excavations for gravel and recreational development of the land.

Within this general area, 45 pit-traps were set in groups in diverse places for sampling the substrate invertebrates in a variety of abiotic conditions and community types varying in elevation from 83 m. to 395 m. above sea level. Summary descriptions of these places, on a macrobiotopic level, are given below.

SERIES 1:

(a) Traps 1–3. Open area covered by dense grass between an extensive stretch of closely mowed grass and mixed woods. Milkweed (*Asclepias syriaca* L.) numerous with some goldenrod (*Solidago* ssp.) and blue vetch (*Vicia cracca* L.).

(b) Traps 4–6. Mixed woods consisting of maple (*Acer saccharum* Marsh), basswood (*Tilia americana* L.) and elm (*Ulmus americana* L.). Understory composed of vetch, aster (*Aster* sp.), thistle (*Cirsium* sp.), and juniper (*Juniperus communis* L.). Some cedar (*Thuja occidentalis* L.)

SERIES 2: Traps 7–9. Forest mostly of maple and a few birch (*Betula* sp.). Substrate rocky under thin litter.

SERIES 3:

(a) Traps 10–11. Area dominated by juniper with a few sumach (*Rhus typhina* L.)

(b) Trap 12. Wet area between juniper barren and mixed conifer wood. Willow (*Salix* ssp.) and goldenrod dominant.

series 4: Traps 13–15. Open transition area.

One trap (13) shaded by sumac and surrounded by grass and bracken (*Pteridium aquilinium* (L.)). Two traps unshaded; milkweed dominant emerging from grass and bracken.

series 5: Traps 16–18. Open area created by old gravel excavation; earlier successional stage than Series 4; ground stony; little humus. Cover changes drastically during the year and consists of goldenrod, blue weed (*Echium vulgare* L.) white clover (*Melilotus alba* Desr.) and raspberry (*Rubus* sp.).

series 6:

(a) Traps 19, 19A. Ten meters inside a moist woods consisting mostly of poplar (*Populus tremuloides* Michx.) and ash (*Fraxinus* sp.) (19A). Trap 19 just outside former woods at the edge of an extensive gravel pit which still is used occasionally.

(b) Traps 20–21. In a gravel pit; barren, rocky ground with a few sumac and some strawberry (*Fragaria virginiana* Duchesne).

(c) Trap 22. On an open sandy rise, not recently disturbed; strawberry numerous; also St. John's wort (*Hypericum perforatum* L.) and goldenrod.

series 7: Traps 23–25. Open area completely surrounded by woods and covered by grass with aster, goldenrod, and timothy (*Phleum pratense* L.) abundant. Trap 23 at edge of woods.

series 8: Traps 26–28. High wooded hill (395 m. above sea level); traps 26 and 27 on the western exposure of the hill; ground covered mostly by *Carex* sp.; trees consisting of stunted maple, ash, and oak (*Quercus* sp.). Trap 28, 20 m. from exposed western edge; trees taller including oak, maple, ironwood (*Ostroya virginiana* (Mill.)).

series 9: Traps 29–31. At the foot of the former hill under mature maple and beech (*Fagus grandifolia* Ehrh.) with numerous maple saplings.

series 10: Traps 32–34. In a damp woods dominated by paper birch (*Betula papyrifera* Marsh) and some maple saplings.

series 11: Open area, partly cultivated.

(a) Traps 35–37. One trap (35) in a grassy clearing surrounded by willow; goldenrod very numerous in summer (100+ plants per m^2) reaching a height of 1–2 m. Trap 36, in damp ground among and shaded by willows, 2–3 m. tall. Trap 37, two meters from a hay field; damp ground completely covered by sensitive fern (*Onoclea sensibilis* L.).

(b) Traps 38–41. Cultivated hay field consisting mostly of timothy and including a few scattered milkweed and vetch; hay mowed once per year in August. Trap 41, just outside hay field in recently uncultivated ground surrounded by juniper, apple (*Malus* sp.) and small elm; low grass cover.

SERIES 12: Traps 42–44. A stand of mature white pine (*Pinus strobus* L.), 20–30 m. tall; undergrowth of numerous maple saplings; litter mainly pine needles; soil relatively dry.

CENSUS METHOD

Populations were studied by pit-trapping, using modified plastic flower pots as traps. Each trap was 20.3 cm. in diameter at the top rim and 19.7 cm. deep. Three holes in the bottom of each trap covered with small mesh plastic screen served for drainage. A wire screen platform on metal legs was placed in the bottom of each trap. The screen mesh was large enough to allow insects to fall through to the bottom of the trap but small enough to exclude possible predators such as mice and shrews. To prevent insects escaping from the trap, a ring of commercial heat-stable silicon grease was placed around the inside wall a few centimeters below the top rim. Preliminary experiments showed that this presented an effective barrier to most insects except those with very long legs, such as Opilionidae and jumping insects which might escape without encountering the grease. A rain-shield consisting of a transparent plexiglass disc, about 23 cm. in diameter, elevated on metal legs several cm. above the ground was placed over the top of each trap.

Traps were emptied once each week. The catch was preserved in 70% alcohol with a small amount of glycerine added to keep specimens pliable for subsequent dissection.

Reproductive condition was determined by dissecting females and examining the ovaries. In 1968, the number of mature eggs in the oviducts was also counted. The elytra and wings were displaced laterally and the thin, dorsal body wall cut around the edges and folded back to reveal the ovaries. These lie ventral to the digestive tract but are usually easily visible when the intestine is slightly displaced laterally. Three reproductive categories were recognized: (1) mature females containing mature ova in the oviducts, (2) teneral females without mature ova, (3) spent females without mature ova. The latter two categories can be distinguished by the presence or absence of a so-called "corpus luteum" in the pedicel of the ovariole. In these beetles, the ovarioles are of the polytrophic type in which the eggs alternate with nutritive cells. The "corpus luteum" consists of the yellowish brown remnant of these trophic cells which accompanied the egg during its descent from the ovariole and which remains behind when the mature egg enters the oviduct. In females which have oviposited previously, the "corpora lutea" are usually clearly visible under low power magnification, as an interrupted dark band across the base of each ovary. The

Table 1. Total number of *Pterostichus* trapped, 1966–1969. Figures in parentheses are estimated numbers for 1966 if trapping had begun before May 30, 1966.

Species	Year 1966	1967	1968	1969
P. melanarius	582	342	300	345
P. coracinus	110 (111)	93	91	110
P. lucublandus	262 (301)	217	259	299
P. pensylvanicus	143 (194)	167	346	352
P. mutus	47 (62)	37	40	57

lateral oviducts of spent females are also much broader and more flaccid than those of teneral females.

An index of sexual activity was obtained for the 1968 catch by examining the spermathecae of females for presence of sperms. Spermathecae were extracted and placed successively in absolute alcohol and acetone for several minutes then washed in xylene and mounted on slides in permanent mounting medium.

In four of the five species, the spermatheca is an obvious, more or less finger-shaped structure lying ventral to the digestive tract in the posterior part of the abdomen. It can be readily located by displacing the posterior part of the hind gut dorsally. With the specimen emersed in alcohol, the spermatheca and its duct and the spermathecal gland and duct usually protrude dorso-laterally, and always on the right side, from the base of the vagina near where the latter connects to the median oviduct. There is considerable variation between different species, however, in shape of the spermatheca and in length and point of connection of the spermathecal and glandular ducts. In *P. lucublandus*, the spermatheca is particularly difficult to locate as it is closely apposed to, and curling around, the base of the vagina.

PHENOLOGY

The total number of individuals of each species trapped during four consecutive years is shown in Table 1. Trapping in 1966 began May 30 by which date at least three of the species had been active for some time. The numbers in parentheses in Table 1 represent the approximate numbers which might have been obtained if trapping had included the total active period of each species. The upward adjustment represents the average percent of each species trapped before May 30 in other years.

Populations of all species decreased to varying extents from 1966 to 1967. Based on the adjusted catch for 1966, *melanarius* decreased by 41%, *mutus* 40%, *lucublandus* 28%, *coracinus* 16%, and *pensylvanicus* 14%. This decline could have been due to the cold winter and spring of 1966–67 but it could also be ascribed to a trapping artifact which will be discussed later. Except among *melanarius*, numbers caught had returned by 1969 almost to the estimated 1966

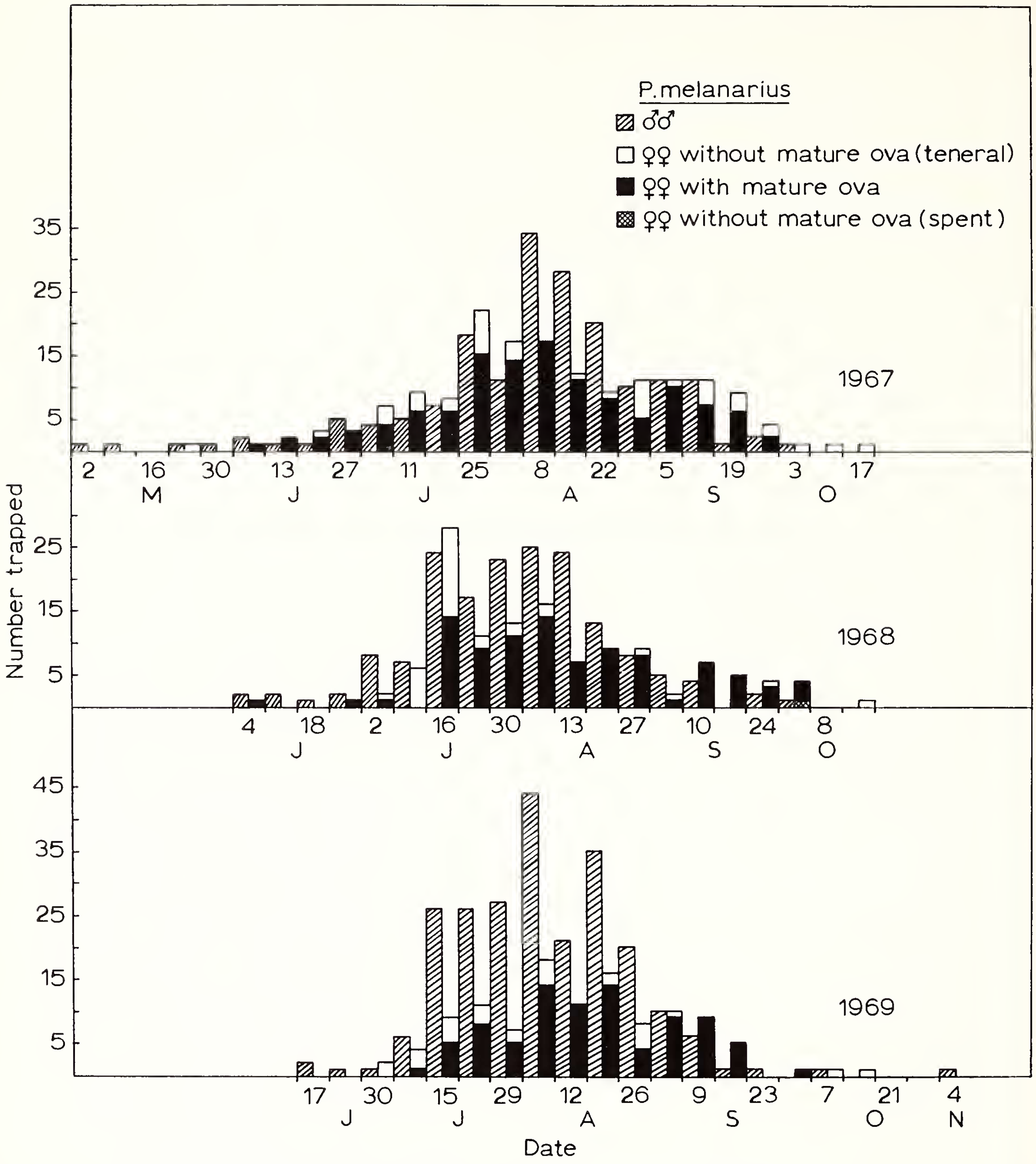

FIG. 1. Number of adult *P. melanarius* trapped per week, 1967–1969.

catch. Only *pensylvanicus* had increased beyond the 1966 level; the 1969 catch was about double that in 1966.

Figs. 1–5 show the number of adults of each species trapped per week during 1967 to 1969 inclusive and the reproductive condition of the females. The 1967 population was not examined for the presence of spent females. Data for 1966 are not included because they are incomplete for some species before May 30. Numbers are from the week ending with the given date and reflect both the absolute number of individuals in the population and the activity of those in-

TABLE 2. Number of teneral females as percentage of total females trapped during 1968.

Date	Species				
	P. melanarius	*P. coracinus*	*P. lucublandus*	*P. pensylvanicus*	*P. mutus*
April 9	–	–	–	50	–
16	–	–	–	75	0
23	–	–	80	29	0
30	–	–	33	25	–
May 7	–	–	10	0	–
14	–	–	13	0	0
21	–	–	0	0	0
28	–	–	0	0	–
June 4	0	–	0	0	0
11	–	–	0	25	0
18	–	0	10	25	33
25	0	0	0	14	–
July 2	50	0	0	0	–
9	100	100	25	16	–
16	50	50	40	100	–
23	20	25	50	–	–
30	15	50	100	–	–
Aug. 6	13	0	100	–	–
13	0	0	–	–	–
20	0	–	–	–	–
27	11	66	0	0	–
Sept. 3	50	0	0	0	–
10	0	0	0	–	–
17	0	–	0	0	–
24	25	–	0	0	0
Oct. 1	0	–	0	0	0
8	–	–	–	0	–
15	100	–	0	0	–

dividuals. Larvae of these species are mostly subterranean and therefore not caught by pit-trapping.

P. melanarius

Adults of this species had one activity-abundance cycle per year which typically began late in May and ended in October (Fig. 1). These dates were somewhat variable but the greatest numbers occurred through July and August. Peak numbers were realized about three weeks earlier in 1968 than in the other two years. This reflects the influence of temperature on rate of maturation and activity of members of the population. Weekly mean temperatures, from hourly readings recorded at ground level between March 1 and April 16, were consistently 1° to 9° higher in 1968.

This species is a summer-autumn breeder. Approximately the same phenological pattern was evident in the population each year. Gravid females were present throughout the whole activity cycle but the proportion of gravid to teneral females varied during the cycle. The species overwinters as larvae as recorded by Greenslade (1965) although some adults may also overwinter. The few gravid females trapped in June most years may have overwintered as adults. In early July, a proportion of teneral females with small, immature ovaries occurred in the population (Table 2). These were probably derived from individuals which had overwintered as larvae. This proportion later decreased and most females trapped subsequently were gravid. This suggests that most progeny from this generation do not mature but overwinter as larvae because it is unlikely that progeny produced after August would have time to mature before development was halted by cold. However, some teneral females always occurred toward the end of the cycle. These individuals usually had large fat-bodies which may be a preparation for hibernation. Sperm was present in the spermathecae of all three females which occurred at this time in 1968 but the ovaries were immature. There may be a reproductive diapause in a proportion of the population. Greenslade (1965) claimed that some adults of this species may hibernate and breed in a second season.

Some spent females also survive in the population, for a time at least, as evidenced by the one trapped on October 1, 1968. Whether or not they survive the winter and breed the following year as Greenslade (1965) claimed and as is the case with other species (Penney, 1965; Vlijm, 1968) is speculative but there may be more of these females in the population than this one specimen would indicate. Vlijm (1968) noted that locomotor activity of spent *Calathus* females is severely reduced which decreases the frequency with which they are trapped.

P. coracinus

This species also had one activity cycle per year which was essentially similar to *melanarius* and extended from late May or early June until September or October (Fig. 2). Peak numbers usually occurred somewhat earlier than *melanarius*. Initiation of the cycle seems to be influenced by temperature since it began three weeks earlier in spring, 1968, when temperatures were consistently higher than in the other two years. Males occurred two to five weeks earlier than females and were more numerous, particularly early in the cycle.

Reproductively, this species also resembles *melanarius*. It is a summer-autumn breeder, gravid females occurring throughout the active period. The proportion of teneral to total females in the population at different times in 1968 (Table 2) indicates that many individuals overwinter as larvae. Young produced by the gravid females which occurred late in the activity cycle could not have matured before winter and must have overwintered as larvae. Some tenerals did occur late in the cycle however, particularly in 1967, 1969, and during the week

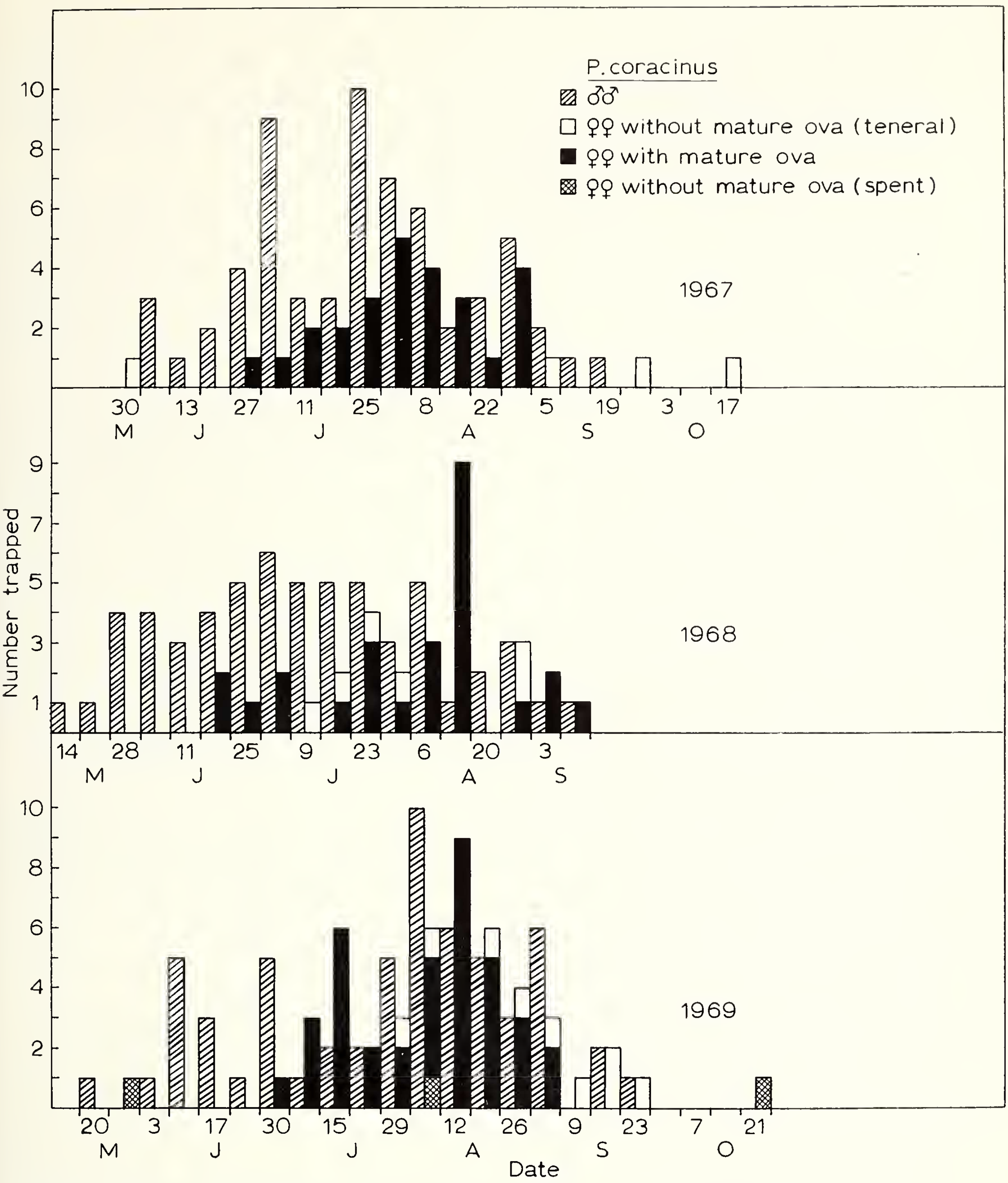

Fig. 2. Number of adult *P. coracinus* trapped per week, 1967–1969.

preceding August 27, 1968. Both teneral females trapped at this time in 1968 contained sperm and stored fat. A proportion of the progeny may mature in the same reproductive cycle but, although they may mate, they do not reproduce during that year but hibernate as teneral females. The one female trapped May 30, 1967, four weeks before the main female component of the cycle, may represent that segment of the population. Lindroth (1966) also reported imaginal hibernation in this species.

Some spent females also overwinter. This is evident from the 1969 data. The first female trapped in spring and the last in autumn were both spent. The early female was caught one month before the appearance of any gravid females so it seems likely that it had overwintered in spent condition. Whether or not such females reproduce a second time is unknown.

Possibly gravid females also overwinter with a full complement of eggs. They more likely oviposit and then either die or hibernate as spent females. The earliest gravid females which appeared in the population may have wintered either as larvae or teneral adults. In the latter case, they must have remained inactive until gravid since males were usually active for four or five weeks previously.

The teneral females trapped during July, 1968 (Table 2) represented about half the adult female population, assuming that gravid and teneral females were equally active and therefore trapped with the same frequency. These tenerals were likely derived from overwintered larvae rather than from eggs laid by the present generation because only one month had elapsed since the appearance of gravid females in the population. This hardly seems time for development from egg to adult. Thiele (1961) recorded two weeks as the minimal duration of even the first larval instar of *P. vulgaris* L. Teneral females trapped after July were likely progeny from the present reproductive cycle.

P. lucublandus

Two cycles per year were distinguishable in this species (Fig. 3). The spring cycle extended from mid-April or beginning of May to beginning or mid-August and the second cycle from mid-August to the end of October. As with *coracinus*, temperature influenced initiation of the spring cycle which began two weeks earlier in 1968 than in the much cooler spring of 1967. The peaks of both cycles also occurred earlier in 1968 than in 1967.

This species is a spring breeder. Gravid females began to appear in the population about two weeks after the beginning of the first cycle. As females matured, the proportion of tenerals in the population decreased (Table 2). From about the third week in May until early July, nearly all females were gravid. Toward the end of the first cycle, the proportion of teneral females again increased. These individuals were probably derived from eggs laid earlier in the same cycle. The fate of these females is uncertain. Eight out of nine of them in 1968 were fertilized and the ovaries were partially developed. If these females survive the winter, they must enter reproductive diapause and hibernate directly. In any case, they do not occur in the second cycle.

All females in the second cycle were sexually immature and many were callows, i.e., newly emerged beetles whose cuticle had not yet hardened. None of the females examined from this segment of the population in 1968 had been fertilized. This cycle is composed entirely of progeny from individuals of the first cycle

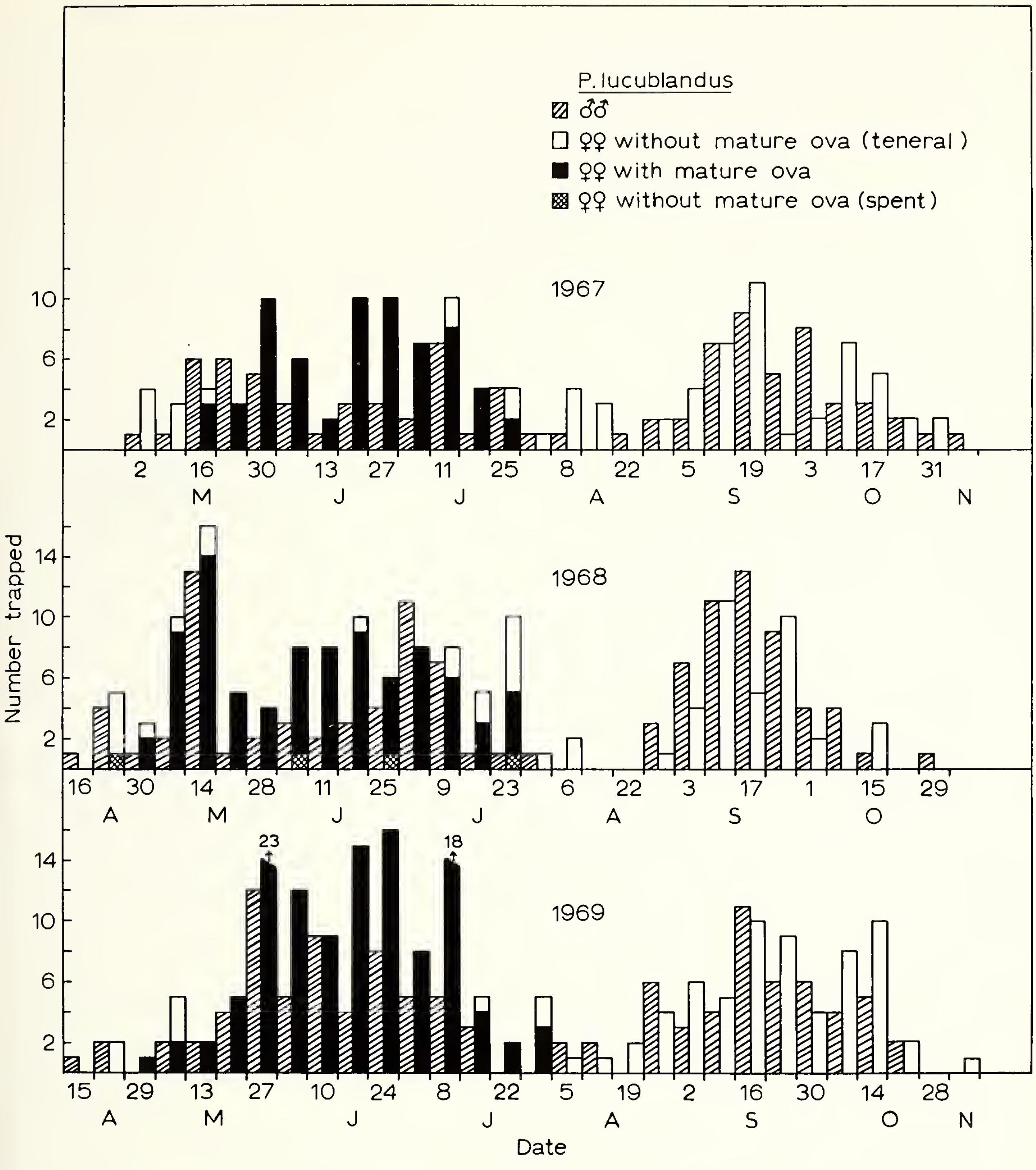

Fig. 3. Number of adult *P. lucublandus* trapped per week, 1967–1969.

and has nothing to do with reproduction. Activity at this time is connected with feeding and the search by newly emerged adults for suitable hibernation sites. These beetles overwinter in reproductive diapause.

A number of spent females was found in the first cycle in 1968 but none in the second cycle. Some spent females from the spring cycle generally must be present, however, and likely overwinter, as evidenced by the one spent female trapped April 23, 1968 before any gravid females had appeared. If locomotor activity of spent females is reduced, as Vlijm (1968) noted for *Calathus*, they may be present in the population during the second cycle but are not trapped.

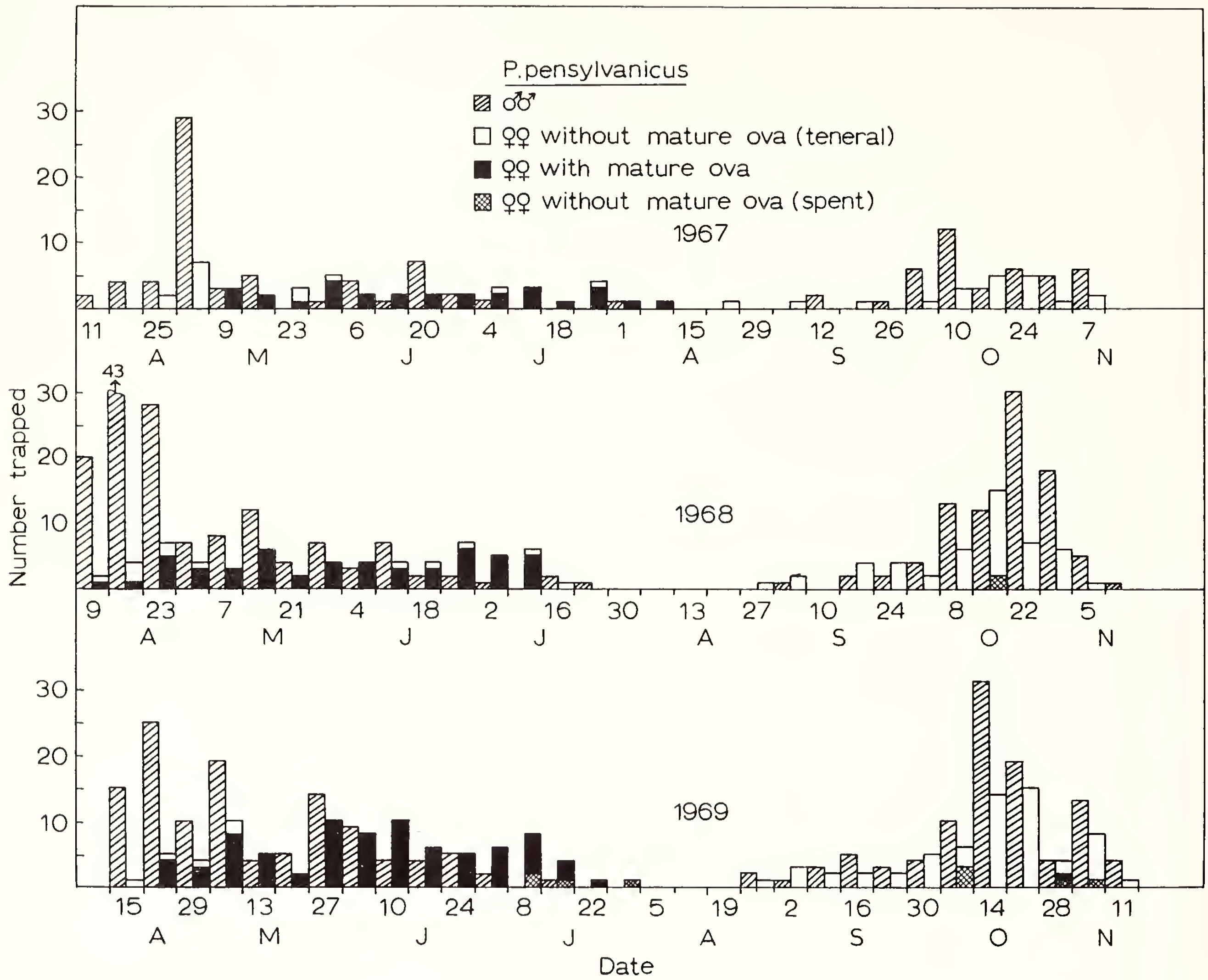

FIG. 4. Number of adult *P. pensylvanicus* trapped per week, 1967–1969.

P. pensylvanicus

This species also had two cycles per year (Fig. 4); the first extended from mid April to mid or end July and the second cycle from early September to the first or second week in November. Males were more active than females during the first few weeks of the spring cycle. Number trapped appeared to be related to temperature. In the exceptionally warm spring of 1968, 50% of the first cycle occurred by April 23; in 1967, 50% occurred nine days later.

Reproduction among *pensylvanicus* occurred in the spring and, as with *lucublandus*, was confined to the first cycle. Most females in the population were tenerals (Table 2) during the first two weeks of their activity in the spring as progressively more females emerged from hibernation. These early tenerals in 1968 carried sperm and the ovaries were already enlarged. During the next six to eight weeks, nearly all females in the population were apparently gravid. The appearance of a small proportion of teneral females after this until the end of the first cycle in 1967 and 1968 reflects the introduction into the population of newly emerged females produced from eggs laid in April and May. Some spent females occurred toward the end of the first cycle in 1969.

Individuals composing the second cycle are derived mostly from eggs laid during the spring cycle. Active females in the second cycle were tenerals with a small proportion of spent females from the first cycle. In 1969, one gravid female was trapped on October 28 for which there is no immediate explanation. One-quarter of individuals of the second cycle were callows and females from this cycle had small, immature ovaries and considerable stored fat. The males also contained large stores of fat at this time. This species overwinters largely as adults, the females as tenerals in reproductive diapause. There is no evidence to indicate whether spent females and larvae overwinter. Considering the relative size of the population which composed the second cycle, it seems that progeny from the spring reproductive cycle complete development before winter.

The autumn cycle of *pensylvanicus*, similar to *lucublandus*, has nothing to do with reproduction but with the search for food and hibernation sites. An essential difference, however, between the two species is that sexual activity may occur during the second cycle in *pensylvanicus*. Sperm was found in the spermathecae of 14 out of 31 females examined from the second cycle in 1968. It is possible that some of these females emerged during the first cycle, were fertilized, then entered reproductive diapause to become active later in the second cycle. All teneral females toward the end of the first cycle in 1968 had been fertilized. However, 70% of a sample of males examined from the second cycle had well developed testes in which sperm were abundant both in the apical portions of the testes and throughout the vasa defferentia. The rest had small, immature testes in which sperm were not obvious. Copulation may occur during this time although this was never observed. The fertilized females of the second cycle had ovaries sufficiently developed to be clearly visible although they contained no mature ova. The unfertilized beetles had immature, inconspicuous ovaries. None of the callow females examined was fertilized. It appears, as was suggested for *melanarius*, that fertilization may stimulate ovarial development but, during this time, development is halted by a reproductive diapause at an immature stage before the maturation of ova.

P. mutus

Phenologically, this species is similar to *lucublandus* and *pensylvanicus*. Two distinct cycles of adult activity occurred per year (Fig. 5). The first cycle began in mid-April and ended usually the first week in July. The second cycle extended from the latter half of September to the first or second week in November.

Reproduction in this species was confined to the spring cycle during which most of the active females in the population were gravid. In 1968, one teneral female was trapped toward the end of this cycle. As with the other species, such individuals represent the new generation from eggs laid earlier in the same cycle.

The second cycle was composed of progeny from the spring cycle. Nearly all

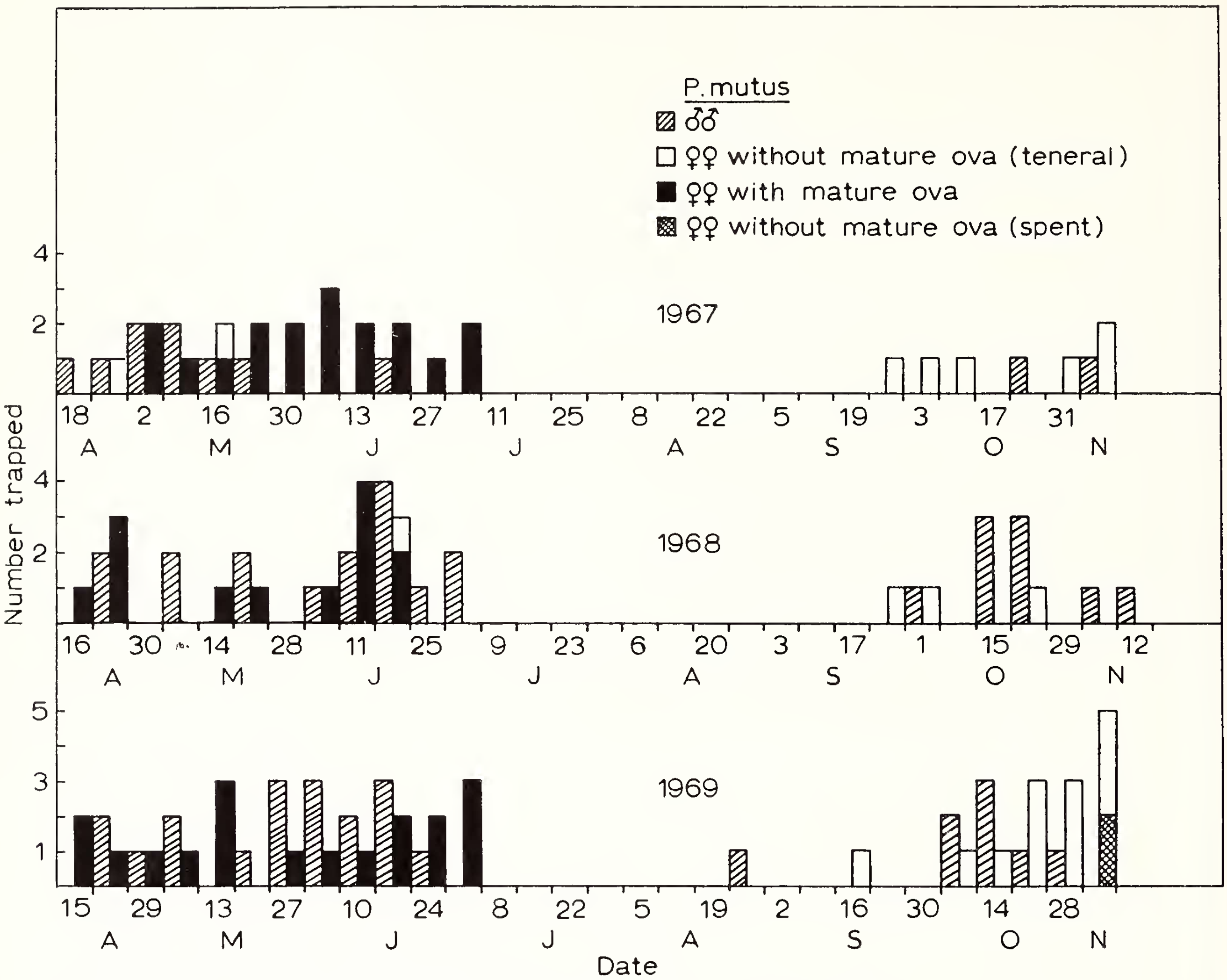

FIG. 5. Number of adult *P. mutus* trapped per week, 1967–1969.

females trapped at this time were sexually immature and unfertilized. Exceptions were two spent females captured at the end of the second cycle in 1969. This indicates that at least a small proportion of females from the spring cycle survive the mid-summer period of inactivity to become active later in the second cycle. Whether or not these individuals overwinter is speculative.

The immature beetles composing this second cycle must certainly overwinter. Both sexes trapped during this time contained large stores of fat, in advance of hibernation.

FECUNDITY

The number of mature eggs per gravid female in the 1968 catch was counted. Since the frequency distribution of egg numbers was not normal, the median egg number was determined, rather than the average, and is shown in Table 3. The maximal number of eggs carried at any one time was found in *melanarius*. It is doubtful, however, whether maxima are valid measures of total fecundity since some eggs may have been laid before capture or more might have been produced subsequently. Most gravid females contained ova in various stages of

Table 3. Median numbers of mature eggs per gravid female during 1968. Numbers in parentheses indicate range.

Species	Median No. eggs
P. melanarius	14 (1–49)
P. coracinus	12 (2–34)
P. lucublandus	12 (1–34)
P. pensylvanicus	7 (1–24)
P. mutus	18 (2–25)

development. It therefore seems that the number of mature eggs may provide an estimate of the rate of oviposition.

Fig. 6 shows the median number of mature eggs per gravid female in 1968 plotted against time. Assuming that the number of mature eggs contained is proportional to the rate of egg-laying, this rate remained uniform over much of the reproductive cycle of those species which overwinter principally as teneral adults, i.e., *lucublandus, pensylvanicus*, and *mutus*. Among *melanarius* and

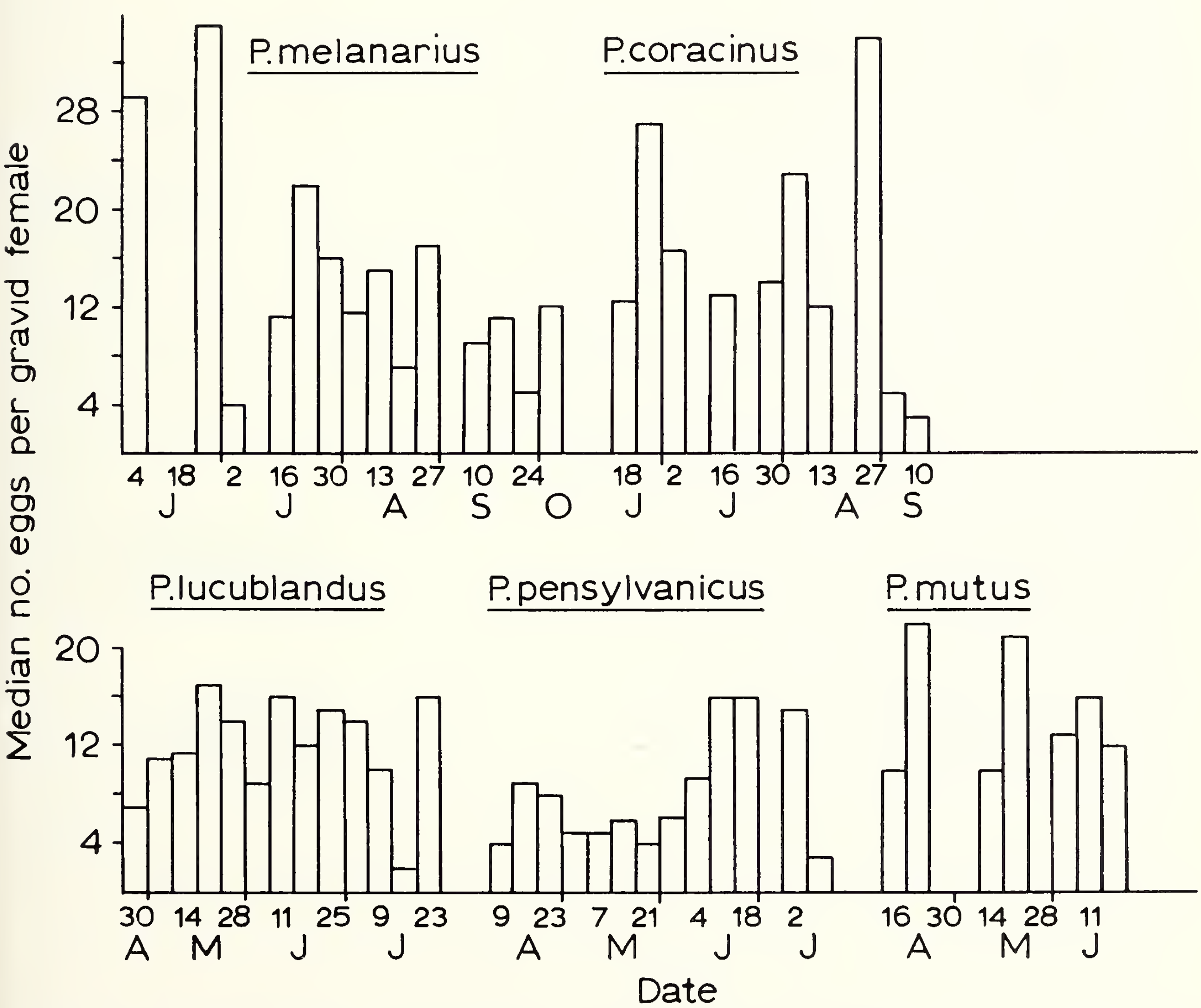

Fig. 6. Median number of mature eggs per gravid female at different times during 1968.

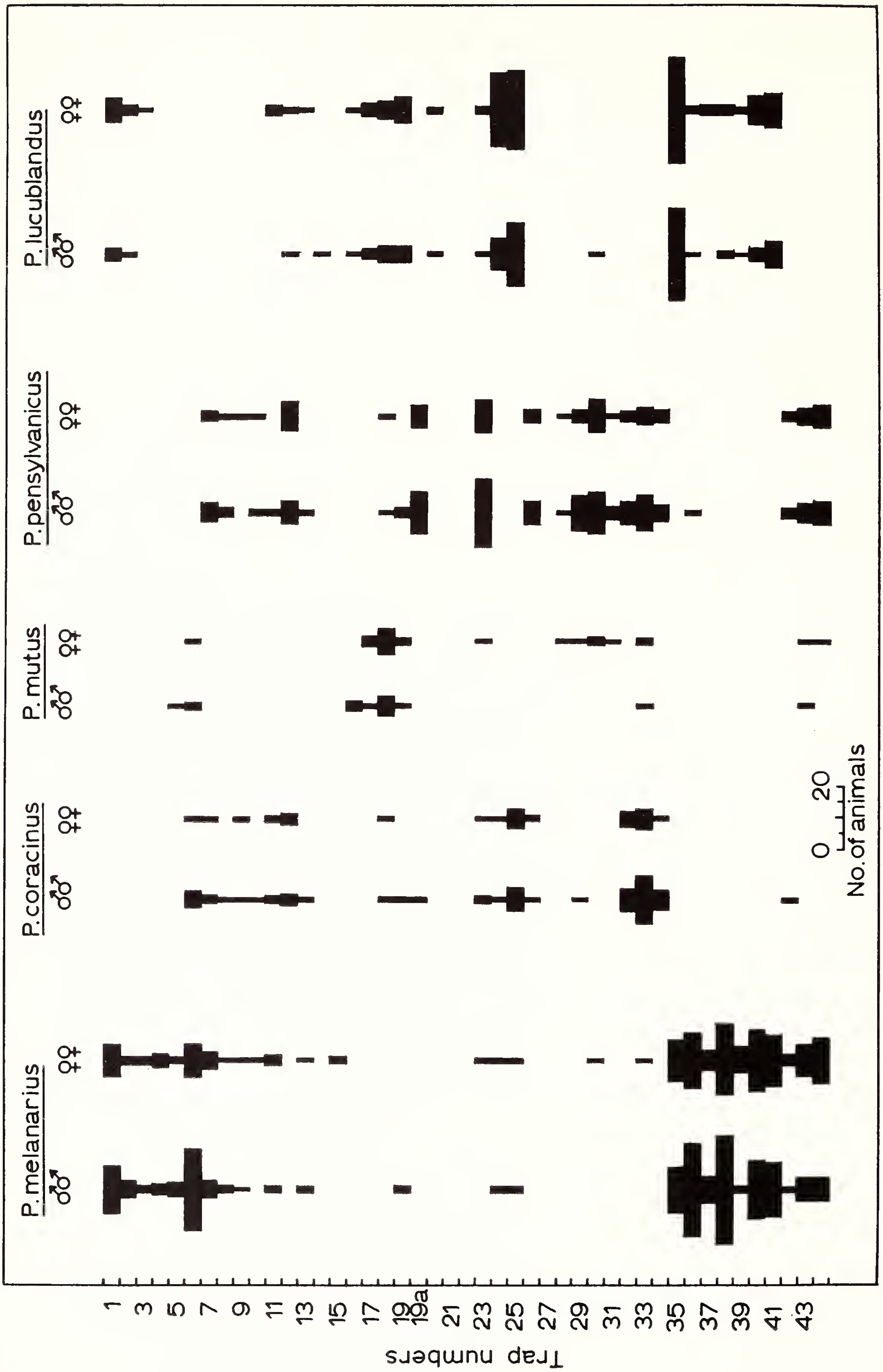

Fig. 7. Mean number of *Pterostichus* adults collected per trap, 1966–1968.

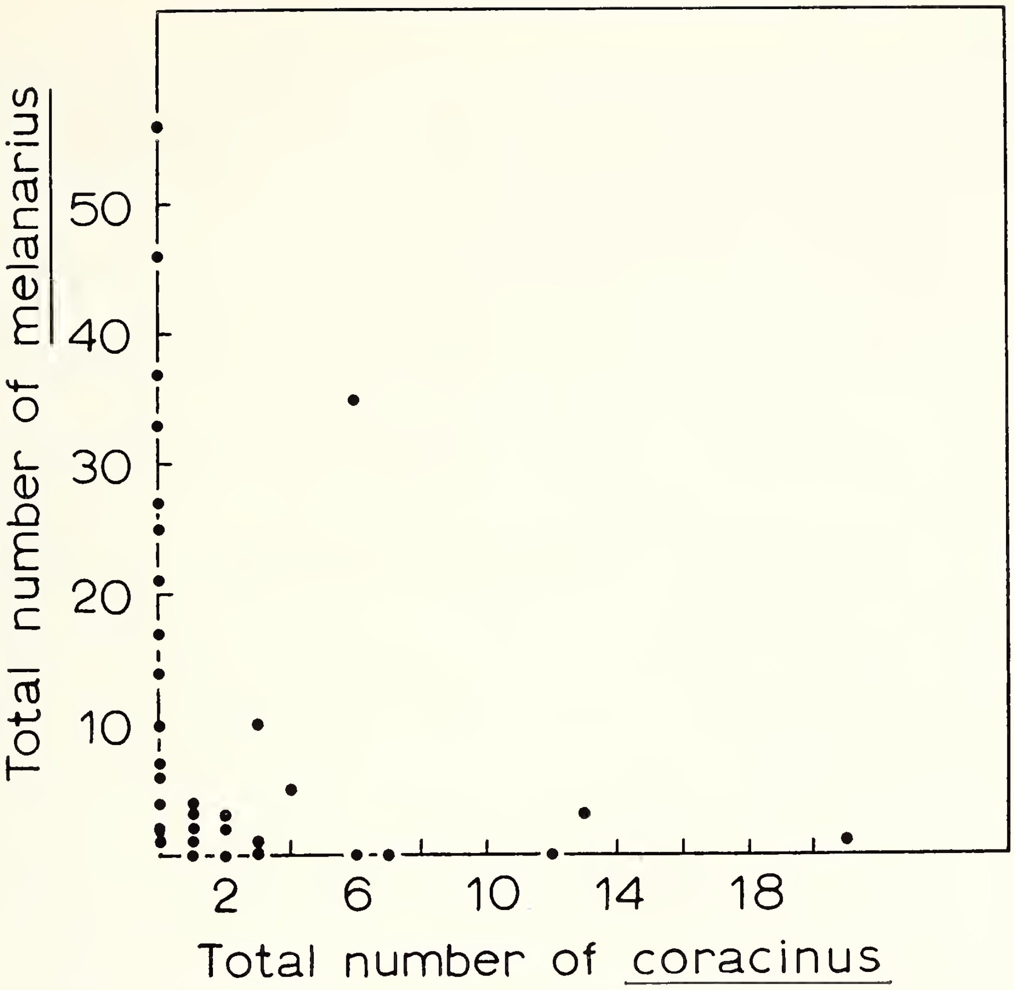

Fig. 8. Relation between total numbers of *P. melanarius* and *P. coracinus* collected per trap in 1968.

coracinus, however, which may overwinter partly as adults, the rate for the first females of the reproductive cycle was high. This suggests that many of these individuals may have overwintered as pre-reproductive adults and therefore reached maximal fecundity rapidly. The median number of eggs subsequently dropped before rising again suggesting the appearance in the population of recently emerged individuals which had overwintered as larvae and therefore were slower reaching maximal oviposition-rate.

ECOLOGICAL DISTRIBUTION

Fig. 7 shows the average number of adults of each species collected in each trap over the years 1966 to 1968 inclusive. The distributions of the sexes, in each case, were similar. No significant seasonal differences in distribution were observed.

P. melanarius

This species occurred in open or semi-open country and in both cultivated and uncultivated land. It was also found in deciduous and coniferous forests. It avoided barren places and preferred areas with deep, rich soil.

P. coracinus

Most individuals of this species were trapped in forest or forest edge and damp poorly drained soil. It avoided open, dry places but occurred to some extent on rocky, shallow soil as not completely devoid of vegetative cover. It was not found in cultivated terrain.

At least on a quantitative basis, and granting the intrinsic difficulties of making numerical comparisons from pit-trap data, *coracinus* and *melanarius* appear negatively associated. The greatest numbers of each species occurred where the other was scarce or absent, with one exception (Trap no. 6). For both open grassland and woods, where *melanarius* was numerous, *coracinus* was absent and where *melanarius* was scarce, *coracinus* was numerous (Fig. 8).

At present, it is speculative whether or not this differential distribution is the result of competitive displacement or merely the response to different environmental requisites. There is reason to believe that some form of mutual interference may occur between these two species. They are similar in both external and internal form and in some aspects of their ecological relations. However, *melanarius* is an introduced species which is spreading rapidly into areas occupied by *coracinus* (Lindroth, 1966). The solution of this problem requires further information on the ecology, particularly the feeding habits, of the two species.

P. mutus

This species was found in both coniferous and deciduous woods or at the edge of woods but occasionally in partly open country with sandy, humus-deficient substrate. It avoided open grassland.

P. pensylvanicus

This is a typical forest species; the greatest numbers were trapped in forest or forest edge. The limiting factors in distribution seem to be some characteristics of high forest, such as cover or presence of litter. It avoided open areas and even open areas covered by long grass. The distribution may be restricted by light. Thiele (1964) determined experimentally that, among 23 species of Carabidae, the determining factors in the distribution of most forest species were light and humidity.

P. lucublandus

This is the only species which was restricted to open country or forest edge. Only one specimen in three years was taken within a deciduous forest. It avoided barren ground but occurred in areas with rich grass cover. Preliminary observations suggest that this species is diurnal in activity and that the other four species are nocturnal.

DISCUSSION

Much has been written about the efficiency of pitfall traps in providing quantitatively valid population estimates. Greenslade (1964) noted weaknesses in this method which are applicable to carabid populations. Briggs (1961) concluded that the number trapped has little relation to the actual size of the population. But Banerjee (1970) has shown, at least with millipedes, that there is a direct relationship between density of animals and the number trapped up to a level of about 200 individuals per 81 m^2 which is probably above most naturally occurring millipede densities. However, he did not mention the type of terrain on which his experiments were conducted and this may also influence the catch.

Another inaccuracy inherent in pitfall data occurs if trapped individuals are not released. When numbers are compared in successive generations of the same species, the number of individuals extracted from the population in generation n may be expected to reduce the number of individuals in the population and therefore the catch in generation $n + 1$. This may be especially true of isolated populations which reproduce slowly and change little due to emigration or immigration. The reduction in numbers trapped among *Pterostichus* species from 1966 to 1967 could be ascribed to this trapping artifact. Nothing is known about the mobility of these populations but the amount of immigration might effect the speed at which and extent to which populations subsequently return to their initial size. Similar observations were made by Barlow (1957, 1958) on millipede populations. Briggs (1961), however, found no depletion of carabid populations in strawberries due to trapping. In any case, caution is necessary when interpreting pit-trap data.

The main difficulty in explaining phenological changes is to separate the activity and abundance components of the population which influence numbers trapped. There is some indication that initiation of activity in the spring among these species is partly due to the effect of temperature on emergence of adults from hibernation or the metamorphosis of overwintered larvae. The decline in numbers in the fall is no doubt partly due to progressive reduction in locomotor activity with falling temperature and the beginning of hibernation. Added to this, among the summer breeders at least, must be the death of a proportion of the spent individuals.

Reduction of numbers during mid-summer among the spring breeders with two cycles per year is due largely to the inactivity and/or death of spent individuals from the reproductive cycle before emergence of the main body of young beetles of the autumn cycle. Larsson (1939) noted among Danish spring breeders that the old beetles died rapidly after reproduction. However, it is unlikely that this is the only reason for the mid-summer decline in occurrence since there is evidence (Figs. 3, 4, and Table 2) in both *lucublandus* and *pensylvanicus* that young imagines are active toward the end of the spring reproductive cycle. The fate of these individuals is unclear. Among *pensylvanicus,* they may become active again during the autumn cycle. With *lucublandus,* this does not happen; so if these beetles survive, they must enter hibernation directly. This would account for their disappearance at this time. Also, the occurrence of spent *pensylvanicus* and *mutus* females during the autumn cycle indicates, that some individuals which were active during the spring cycle survive the summer decline and resume activity later. These individuals, however, form only a small proportion of the autumn peak which consists of newly emerged adults seeking hibernation sites. The mid-summer decline in numbers may be caused by several factors. Among some carabids with two cycles per year and which breed during the second cycle, the reduction of activity in mid-summer can be ascribed to a diapause of the total adult population (Penney, 1966). With *Pterostichus,* however, the situation is complicated by the juxtaposition of two successive generations around the summer decline.

The observed breeding periods agree with information previously published for most of these species. One exception is Rivard's (1964) observation of gravid female *pensylvanicus* in August, September, and October. With one exception during the present work, only young, sexually immature *pensylvanicus* females were found at that time.

Pterostichus seem to be spring breeders which overwinter as adults. Ten of the 14 species described by Larsson, (1939), Dawson (1965), Greenslade (1965), and the present work are in this category. These species have two activity-abundance cycles per year although this characteristic is variable depending on geographic distribution, (Greenslade, 1965). The remaining four species are summer-autumn breeders, with one cycle per year, which overwinter as larvae although *melanarius* and *coracinus,* hibernate more or less frequently as adults. Larsson (1939) noted that although such "Herbsttieren" overwinter mainly as larvae, a certain proportion of adults also overwinters but these die before the next breeding period.

The maximal number of mature eggs counted in any one female was higher than Rivard's (1964) records. However, this could be a function of the collecting techniques. Rivard used pit-traps but emptied them twice per week. In this study they were emptied only once per week. If females develop and lay eggs intermittently over a period of time, they may continue to produce mature eggs after falling into a trap but retain them because they lack the stimulus of a suitable oviposition site. Thus, the number of mature eggs can be expected to be greater if collections are made once rather than twice per week.

Since eggs may not be laid all at once, the average or median number of eggs may be a more meaningful indication of potential fecundity of these species. Murdoch (1966) stated that, with some *Agonum,* the number of mature eggs in a female was proportional to the rate at which it was ovipositing. He also observed that eggs in all stages of development were present in gravid females. In addition, he found a correlation between mature egg number and subsequent number of larvae and new adults. Briggs (1957) and Penney (1966) reported that other Carabidae oviposit intermittently over an extended time.

Comparing Tables 1 and 3 emphasizes that median fecundity bears little relation to the absolute size of any species population in an area, assuming that numbers trapped are a valid indication of that size. *P. mutus*, which had the highest median fecundity in 1968, had the smallest population. The reverse was true of *pensylvanicus*. The value of observations of fecundity is restricted to assessing possible changes in numbers in successive generations of the same species and in determining times of maximal reproduction.

The present observed distributions agree with reports on the same species by Lindroth (1966) and Rivard (1964). Minor exceptions are Lindroth's record of *coracinus* in open fields and meadows and Rivard's account of the same species on dry soil. During the present study, *coracinus* was not observed in open, dry places.

Greenslade (1965) and Thiele (1964) noted connections between temporal-spatial distribution of carabids and their breeding type. Greenslade reported that winter larvae and late summer activity predominate among species in woodland habitats whereas there is earlier activity and greater adult over-wintering of species in grassland. The present species do not entirely conform to these generalizations. *P. pensylvanicus* is confined to wooded areas, over-winters in the adult stage, and is active early in the spring. The other woodland species, *coracinus*, is not typically active in late summer.

Among the species which Thiele (1964) studied, spring breeders occurred only in cool, moist forests. The explanation given for this was that the vulnerable larval stages occurred in summer, the time of greatest heat and dryness. Therefore, the species were restricted to moist, cool places. The larvae of autumn breeders, however, were present when the weather was cooler and damper. Such species, therefore, were not confined to woods. Two of the present five species, *lucublandus* and *coracinus* do not comply with this pattern; *lucublandus* is a spring breeder found in open country; *coracinus* is a summer breeder and occurs in forest or forest edge. It is doubtful whether such temporal-reproductive relationships have much influence on the distribution of these species because their larvae are mostly subterranean and therefore protected from excessive heat and desiccation.

Larsson (1939) also recorded correlations between distribution and phenological relationships of Danish carabids. Among the group which he designated as "Herbsttieren," i.e., those which breed in summer and autumn, he reported that the reproductive maximum occurred earlier in forest biotopes. This was due to the winter temperature being less severe in woods than in open areas thereby permitting more rapid maturation of overwintered larvae. This relationship could not be verified in the present work. With *melanarius*, which inhabits both wooded and open areas, no consistent difference was evident in timing of reproductive cycles in the two segments of the population which occurred in these two habitat types.

Literature Cited

BANERJEE, B. 1970. A mathematical model on sampling diplopods using pitfall traps. Oecologia (Berl.) **4**: 102–105.

BARLOW, C. A. 1957. A factorial analysis of distribution in three species of diplopods. T. Entomol. **100**: 349–426.

———. 1958. Distribution and seasonal activity in three species of diplopods. Arch. néerl. Zool. **13**: 108–133.

BRIGGS, J. B. 1957. Some experiments on control of ground beetle damage to strawberry. Rep. E. Malling Res. Stn. 1956, 142–145.

———. 1961. A comparison of pitfall trapping and soil sampling in assessing populations of two species of ground beetles (Col.: Carabidae). Rep. E. Malling Res. Stn. 1960, 108–112.

DAWSON, H. 1965. A comparative study of the ecology of eight species of fenland Carabidae (Coleoptera). J. Anim. Ecol. **34**: 209–314.

GREENSLADE, P. J. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). J. Anim. Ecol. **33**: 301–310.

———. 1965. On the ecology of some British carabid beetles with special reference to life histories. Trans. Soc. Brit. Entomol. **16**: VI, 149–179.

LARSSON, S. G. 1939. Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden. Entomol. Medd. **20**: 277–560.

LINDROTH, C. H. 1966. The ground-beetles of Canada and Alaska. Part 4, Opusc. Entomol. suppl. **24**: 409–648.

MURDOCH, W. W. 1966. Aspects of the population dynamics of some marsh Carabidae. J. Anim. Ecol. **35**: 127–156.

PENNEY, M. M. 1966. Studies on certain aspects of the ecology of *Nebria brevicollis* (F.) (Coleoptera, Carabidae). J. Anim. Ecol. **35**: 505–512.

RIVARD, I. 1964. Carabid beetles (Coleoptera: Carabidae) from agricultural lands near Belleville, Ontario. Canadian Entomol. **96**: 517–520.

THIELE, H. U. 1961. Zuchtverzuche an Carabiden, ein Beitrag zu ihrer Ökologie. Zool. Anz. **167**: 431–442.

———. 1964. Experimentelle Untersuchungen über die Ursachen der Biotopbindung bei Carabiden. Z. Morph. Ökol. Tiere **53**: 387–452.

VLIJM, L., TH. S. VAN DIJK, AND S. Y. WIJMANS. 1968. Ecological studies on carabid beetles. III. Winter mortality in adult *Calathus melanocephalus* (Linn.), egg production and locomotory activity of the population which has hibernated. Oecologia (Berl.) **1**: 304–314.